A global analysis of terrestrial plant litter dynamics in non-perennial waterways

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Abstract: Perennial rivers and streams make a disproportionate contribution to global carbon (C) cycling. However, the contribution of intermittent rivers and ephemeral streams (IRES), which sometimes cease to flow and can dry completely, is largely ignored although they represent over half the global river network. Substantial amounts of terrestrial plant litter (TPL) accumulate in dry riverbeds and, upon rewetting, this material can undergo rapid microbial processing. We present the results of a global research collaboration that collected and analysed TPL from 212 dry riverbeds across major environmental gradients and climate zones. We assessed litter decomposability by quantifying the litter carbon-to-nitrogen ratio and oxygen (O2) consumption in standardized assays and estimated the potential short-term CO2 emissions during rewetting events. Aridity, cover of riparian vegetation, channel width and dry-phase duration explained most variability in the quantity and decomposability of plant litter in IRES. Our estimates indicate that a single pulse of CO2 emission upon litter rewetting contributes up to 10% of the daily CO2 emission from perennial rivers and stream, particularly in temperate climates. This indicates that the contributions of IRES should be included in global C-cycling assessments.

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A global analysis of terrestrial plant litter dynamics in non-perennial waterways

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Perennial rivers and streams make a disproportionate contribution to global carbon (C) cycling. However, the contribution of intermittent rivers and ephemeral streams (IRES),

which sometimes cease to flow and can dry completely, is largely ignored although they represent over half the global river network. Substantial amounts of terrestrial plant litter accumulate in dry IRES and, upon rewetting, this material can undergo rapid microbial processing. We present the results of a global research collaboration which collected and analysed terrestrial plant litter from 212 IRES reaches spanning major environmental gradients and climate zones. We assessed litter decomposability by quantifying the litter C-to-nitrogen ratio (C:N) and oxygen (O_2) consumption in standardised assays and estimated potential short-term CO_2 emissions during rewetting events. Aridity, cover of riparian vegetation, channel width, and dry phase duration explained most variability in the quantity and decomposability of plant litter in IRES. Our estimates indicate that IRES contribute up to 10% of stream and river CO_2 evasion, through pulses of CO_2 emission upon litter rewetting, particularly from temperate climates. Incorporation of IRES has become pivotal to improve the accuracy of global C cycling assessments.

Decomposition of terrestrial plant litter is an essential, biosphere-scale ecosystem process[1]. Of 120 Pg of organic C produced by terrestrial plants annually, about half is respired by the plants but only a small fraction is removed by herbivores, so that up to 60 Pg enter the dead organic matter pool[1,2]. Fresh waters make a disproportionate contribution to global C cycling through terrestrial plant litter (TPL) decomposition and atmospheric CO_2 emissions[3,4]. This contribution is particularly apparent in perennial rivers and streams, where water and nutrient availability stimulate rapid decomposition by microbes and invertebrate detritivores[1,3,5]. TPL deposited in fresh waters, and the release of its decomposition products, are critical energy sources that support food webs and ecosystem processes, including key C cycling pathways[1,5].

A major shortcoming of current estimates of the contribution of rivers and streams to global C cycling[3,6,7] is the omission of IRES, in which drying and rewetting events create ecosystems that transition between terrestrial and aquatic phases[9,10,11]. IRES are widespread ecosystems draining a large proportion of terrestrial biomes across all continents and climate types[8,10,11,12]. Moreover, IRES are increasing in extent due to global change[9,13]. During the dry phase, TPL deposited on the riverbed accumulates, decomposing only slowly through photodegradation and terrestrial decomposer activity[14,15]. Then, when flow resumes, the accumulated material is mobilised and transported downstream[16,17] (**Supplementary Material 1**). Concentrations of particulate and dissolved organic matter in advancing wetted fronts exceed baseflow concentrations by several orders of magnitude[16]. IRES have therefore been conceptualised as punctuated biogeochemical reactors[10].

To understand the role of IRES in global C cycling, global-scale data are needed to characterise the variables controlling TPL accumulation in dry channels and its decomposability upon flow resumption. Climate influences the type and productivity of riparian vegetation[18] and the flow regimes of IRES[9,13]. Channel topography and flow conditions, including the timing and duration of dry periods[14], control TPL deposition and retention, with wide channels receiving proportionally less riparian material than narrow ones[19]. TPL decomposability is typically altered during dry phases, due to partial degradation or leaching of labile constituents, relative accumulation of recalcitrant compounds, and impoverishment of nutrients in terrestrial conditions[15,20]. Therefore, we predict that TPL accumulation and decomposability would be a function of climate, riparian vegetation, channel topography, and duration of the dry phase (**Fig. 1**). We explored these relationships by assessing the quantity and decomposability of accumulated TPL in 212 dry river channels

153 located in 22 countries distributed across wide environmental gradients and multiple climate
154 zones[9] (**Supplementary Material 2**).
155
156 **Terrestrial plant litter accumulation in dry riverbeds**
157 Our results refine current understanding of the global distribution and variability in TPL
158 accumulation in IRES during dry phases. The quantity of TPL collected in 212 dry riverbeds
159 (**Supplementary Material 2**) ranged from 0 to 8291 g dry mass m^{-2} (mean $\pm$ S.D. = 277 $\pm$
160 796, median = 102 g m^{-2}; **Table 1**). This material mainly comprised leaf litter (LL) and wood
161 (41% and 39% of the total mass, respectively), whereas herbs, fruits and catkins accounted for
162 <20% of the total mass (**Table 1**). The quantity of LL ranged from 0-963 g m^{-2} (mean $\pm$ S.D.
163 = 88 $\pm$ 139, median = 36 g m^{-2}).
164
165 Relationships between TPL quantity and environmental variables were assessed using
166 Random Forest models (RF), which are highly flexible regression techniques suitable for
167 modelling responses that show complex relationships with environmental conditions (e.g.,
168 climate, riparian zone, flow regime, channel topography). RF based on data from all samples
169 explained 41.4% and 38.3% of the total variance in TPL and LL quantity, respectively (**Table**
170 **2, Fig. 2**). Supporting our conceptual model (**Fig. 1**), aridity, mean annual precipitation,
171 catchment area, and dry period duration were the most important predictors of TPL quantity
172 (**Table 2**). Aridity, river width, riparian cover, time since senescence, and dry period duration
173 were most influential to determine LL accumulation (**Table 2**). LL quantity generally
174 increased with riparian cover and decreased with river width (**Fig. 2**). Relationships with time
175 since senescence, aridity, and dry period duration were more complex. LL quantity decreased
176 as the aridity index increased to 250, increased sharply until it reached 650 and then plateaued
177 (**Fig. 2**). LL quantity also increased almost linearly as dry period duration increased to 200 d,

and then dropped sharply (**Fig. 2**). The quantity of LL fell for 320 days after estimated senescence and then rose slightly (**Fig. 2**).

The greatest quantity of terrestrial material, in particular LL, was reported from first-order, forested, temperate IRES, suggesting these sites are hotspots of organic matter accumulation in dendritic river networks. This finding concurs with patterns predicted by the River Continuum Concept (RCC)[21] but differ from its predictions regarding the fate of TPL entering river channels. According to the RCC, a large portion of TPL entering forested headwaters is immediately processed by heterotrophic microbes and invertebrate shredders, generating significant amounts of fine-particulate organic matter that is exported downstream. In contrast, we found TPL accumulations in dry channels to be greatly increased compared to perennial rivers[9,14], because the absence of flowing water limits biological activity and physical abrasion. During the initial phases when flow resumes, much of this material can then be transported and further processed downstream[10,11,16].

Overall, LL accumulation in IRES matches global patterns in terrestrial inputs[1,20], revealing strong biogeochemical and ecological links between rivers and adjacent terrestrial ecosystems. The positive relationship between the degree of aridity and the quantity of accumulated LL probably reflects water-limited riparian plant growth[22], while the saturating relationship observed above an index value of 700 suggest that, in humid conditions, LL accumulation becomes limited by other factors. LL quantities in dry channels reflect a balance between riparian and upstream inputs, and losses due to dry-phase decomposition and downstream export during phases of flow. Although our results inform estimates of LL accumulation in dry channels, downstream effects of LL transport and processing when flow resumes will also depend on the decomposability of the accumulated organic matter.

Decomposability of accumulated leaf litter

The C:N ratio of LL, as a first proxy of decomposability, ranged from 17 to 154 (mean ± S.D. = 46 ± 23) and was driven by climate, riparian cover, and dry period duration, as predicted by our conceptual model (**Fig. 1**). However, the RF model explained only 14.9% of the total variance in C:N (**Table 2**). The relationship of the C:N ratio with mean annual potential evapotranspiration (PET) was not monotonic in that the C:N ratio increased sharply between about 700 and 900 mm PET $year^{-1}$ and then gradually decreased (**Supplementary Material 3**). The C:N ratio decreased with riparian cover and the aridity index, the latter relationship resembling the reverse of its response to dry period duration (**Supplementary Material 3**). Aridity was an important influence on C:N, with lower ratios reported for low-aridity environments, including tropical conditions, compared to other climate types[20,23]. More research is needed to determine how plant species richness, vegetation structure and functional diversity in riparian zones affect the C:N and decomposability of LL in dry riverbeds.

Decomposability was also related to preconditioning after LL deposition on dry riverbeds. A few days of drying on the riverbed decreased the C:N ratio of LL, whereas longer drying periods resulted in increases, with peaks occurring after ~100 days before C:N declined again, levelling off after 200 days (**Supplementary Material 3**). The increase in C:N with dry period duration suggests that nutrients, along with other soluble compounds, are preferentially leached from LL in dry riverbeds, resulting in litter composed mostly of nutrient-poor structural compounds such as cellulose and lignin[24]. The initial decomposability of LL falling onto dry riverbeds and subsequent quality changes affect decomposition in both the receiving and downstream reaches[16]. Thus, climate change-related extensions of dry periods[13] could

227 increase downstream transport of low-quality LL, with potential repercussions on detrital food
228 webs and associated ecosystem functions and services.
229
230 **Respiration and potential CO_2 release after leaf litter rewetting**
231 We did not determine decomposition rates directly, but used a proxy of terrestrial litter
232 decomposability by measuring oxygen consumption related to rewetting in laboratory
233 conditions. Oxygen consumption rates of rewetted LL ranged from 0.004 to 0.97 mg O_2 g^{-1}
234 dry mass h^{-1} (mean $\pm$ S.D. = 0.36 $\pm$ 0.20, median = 0.29). These values are in the upper range
235 of respiration rates reported from coarse-particulate organic matter in fresh waters and soils
236 (0.009-0.55 and <0.001–0.35 mg O_2 g^{-1} dry mass h^{-1} for fresh waters and soils, respectively;
237 **Supplementary Material 4**). This indicates that rewetting events are associated with intense
238 biological activity, when the highly labile C fuelling the initial respiration after rewetting can
239 be rapidly metabolised by most heterotrophic microorganisms present in the litter[14]. The
240 global RF model explained 36.8% of the total variation in O_2 consumption rates, with the
241 most important predictors being the riparian forest proportion in the catchment, catchment
242 area, the time since senescence, dry period duration, aridity, and the C:N ratio (**Table 2,**
243 **Supplementary Material 5**). Rates increased with catchment area, and decreased with forest
244 proportion, aridity, C:N, time since senescence, and dry period duration. Upon flow
245 resumption, higher microbial respiration rates are triggered when previous drying events are
246 short compared to extended dry phases. The predicted increase in the frequency of drying
247 events[10,13] might thus have strong implications on IRES metabolism and increase their
248 contribution to the global C cycle through CO_2 emissions upon rewetting.
249
250 Our estimates of CO_2 emissions from IRES upon LL rewetting ranged from 0 to 13.7 g CO_2
251 m^{-2} day^{-1} (mean $\pm$ S.D. = 0.88 $\pm$ 1.51, median = 0.42), which is in the upper range of

252 previously reported emission rates from fresh waters and soils (**Supplementary Material 6**).
253 Notably, the highest values are 10 fold higher than those reported in the most comprehensive
254 estimates of CO_2 emission rates available from inland waters[3], in which reservoirs are
255 expected to release up to 0.34 mg CO_2 m^{-2} day^{-1} and perennial streams up to 1.75 mg CO_2 m^{-2}
256 day^{-1}. Our highest potential short-term CO_2 emission rate associated with litter rewetting
257 could thus represent up to 152% of previous estimates from perennial streams and rivers (min
258 = 0%, mean = 3-10%, max = 47-152%; **Supplementary Material 7**). This is remarkable,
259 especially since our estimates are conservative, because they are mainly based on microbial
260 activity on LL and exclude sediment respiration. The highest emission rates were found at
261 sites characterised neither by the highest O_2 consumption rates nor by the highest quantities of
262 accumulated LL, indicating that the two variables are uncorrelated. This highlights the need to
263 consider both LL quantity and decomposability, to evaluate the role of IRES in the global C
264 cycle.
265 The RF model explained 34.9% of the total variation in the potential CO_2 released and
266 estimated time since senescence, aridity, and drying duration as the most important predictors
267 (**Table 2, Fig. 3a**). Relationships were typically non-monotonic. The CO_2 released decreased
268 sharply until 85 days after estimated senescence, before remaining relatively low and stable
269 (**Fig. 3a**). CO_2 release decreased till an aridity index value of 230, then increased sharply till
270 700 to decrease again and stabilise at values above 800 (**Fig. 3a**). Last, rates of CO_2 release
271 remained stable for 200 d of dry riverbeds, but sharply decreased thereafter (**Fig. 3a**).
272 Although IRES release CO_2 during both flowing[3,25] and dry[26] phases, our study suggests that
273 early stages of rewetting can be considered hot moments[8,10] or control points[27] of CO_2 release.
274 This finding is important because global estimates of CO_2 release focusing on perennial
275 rivers[3,4,7,25] have missed emissions from at least 84,000 km^2 of river channels by overlooking
276 IRES[3,28].

277

278 **Differences among climate zones**

279 Our global study demonstrates that the quantities of organic material accumulating during dry
280 phases in riverbeds vary substantially among climate zones. Temperate IRES accumulated
281 more LL (mean ± S.D. = 97 ± 152, median = 41 g dry mass m^{-2}) than those in the tropics
282 (mean ± S.D. = 32 ± 44, median = 9 g dry mass m^{-2}) and arid climates (mean ± S.D. = 45 ±
283 64, median = 7 g dry mass m^{-2}) (ANOVA, $P < 0.001$). Of the sampled riverbeds, 150, 31, 19,
284 and 10 were located in temperate, arid, tropical and continental climates, respectively,
285 reflecting the geographical spread of current IRES research[29] and highlighting that our results
286 need to be interpreted with caution in less well-represented climate classes, particularly in
287 alpine (only a single location), continental and, to a lesser extent, tropical IRES. When run
288 separately for different climate zones, RF model performance to predict the quantity of
289 accumulated LL was indeed much higher for temperate and arid (36.1% and 26.8% of total
290 variance explained, respectively) than for tropical (5.6%) climates. Thus, our conclusions are
291 more solid in temperate and arid climates, where IRE are widespread, compared to the
292 tropics[30,31]. For example, IRES represent up to 45% of the hydrological network in temperate
293 France[32] and up to 96% in the arid south-western USA[33, 34]. Tropical IRES often have higher
294 annual LL inputs than temperate forests[35], but our ability to predict their LL accumulation in
295 these riverbeds was reduced, probably because of often continuous leaf fall[36]. This result
296 might indicate that C cycling in IRES is less punctuated in tropical than in other climates,
297 although identical predictors were retained by the respective RF models, indicating that litter
298 accumulation is controlled by common factors across all climatic zones.

299

300 Our findings on LL accumulation were paralleled by estimates of CO_2 release upon rewetting,
301 which were also much higher in temperate (mean ± S.D. = 1.06 ± 1.76 g CO_2 m^{-2}) than in arid

and tropical IRES (0.48 ± 0.68 and 0.28 ± 0.35 g CO_2 m^{-2}, respectively). However, this comparison is influenced by the limited ability of our models to predict CO_2 release from arid IRES (4.4% of the variance explained) compared to temperate and tropical IRES (33.5 and 16.8% of the variance explained, respectively). This may reflect the importance of abiotic processes such as photodegradation for LL decomposition in water-limited river ecosystems[15] or the influence of plant functional traits, not included in our model, that are involved in the protection from desiccation and solar radiation, such as the quantities of waxes and phenolic compounds[37].

Implications and perspectives

Our global study spanning 212 reaches on all continents (i) enabled us to document the extent of global variation in TPL and LL quantity and quality across dry riverbeds, and (ii) revealed high O_2 consumption and CO_2 release rates after LL rewetting, notably in temperate regions. These findings support the notion of IRES as punctuated biogeochemical reactors[10], characterised by distinct phases of C accumulation and processing with much higher temporal variability in process rates than in perennial river ecosystems. Transport distance and site of litter deposition and processing after flow resumes will vary with river morphology and the magnitude of the flow pulse[16]. However, except during extreme flow conditions, much of the mobilised litter will remain in river channels and riparian areas, where it decomposes at rates similar to those in perennial rivers. Since these rates are much faster than in upland terrestrial sites[1,14], these findings suggest that neglecting IRES leads to a notable underestimation of the contribution of the world's river network to the total global CO_2 flux to the atmosphere. Our study suggests that in addition to globally relevant amounts of CO_2 released from IRES during both dry[26] and flowing phases, rewetting events act as hot moments[10] or control points[27]. This would imply upward revision of organic matter transformations and CO_2

emissions from river networks on the global scale, since IRES could increase annual estimates of global CO_2 emissions from streams and rivers by 7-152%, the CO_2 released from LL during a single rewetting event alone contributing from 3 to 10% of this increase (**Supplementary Material 7**). Likewise, taking IRES into account would improve estimates of the consequences of global climate change on C cycling, since IRES are predicted to expand in both time and space[8,10,13].

The data and conceptual framework presented here provide the basis needed to develop models of litter decomposition and C cycling in fresh waters that include IRES. The next steps would be to quantify CO_2 emissions upon flow resumption *in situ*[16] and collect data on LL quantity and decomposability for continental and other climates that are not well represented at present. CO_2 emissions from dry[26] and flowing[3,25] phases then need to be integrated with those during wetting events, and temporal variability (including its dependency on other environmental conditions, such as temperature) be studied for extended periods after flow resumes to build adequate quantitative models of global C cycling that consider the spatio-temporal dynamism of IRES under present and future climatic conditions.

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Competing interests

The authors declare no competing financial interests.

Author contributions

T. Datry, A. Foulquier, R. Corti, D. von Schiller, and K. Tockner assumed responsibility for the overall project planning and coordination. All authors collected plant litter in their countries and processed and analysed this material. The centralised lab analyses were conducted by T. Datry, A. Foulquier, R.Corti, C. Mendoza–Lera, and J.C. Clement. The data compilation and database management was carried out by R. Corti and C. Mendoza-Lera. The data analyses were performed by T. Datry, R.Corti, A. Foulquier, and C. Mendoza–Lera. T. Datry led the writing of the manuscript with A. Foulquier and notable contributions by M.O. Gessner, B. Gücker, M. Moléon and R. Stubbington. All other authors commented on and contributed to revising draft versions.

435 **Table 1: Quantity (g dry mass.m^{-2}) of terrestrial plant litter collected in dry riverbeds**

436 **(Min: minimum, Max: maximum, Mean, S.D.: standard deviation, Fraction: % of the**

437 **total quantity.**

438

Type of material	Min	Max	Mean	S.D.	Fraction (%)
Total plant litter (TPL)	0	8 291	277	796	100
Leaf litter (LL)	0	963	88	139	41
Wood	0	7 812	154	715	39
Herbs	0	500	9	40	7
Fruits	0	351	12	42	4
Catkins	0	41	1	4	1
Miscellaneous	0	561	17	58	8

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Table 2. Detailed results of global Random Forest (RF) models on five response variables. The variables used as predictors are described in Supplementary Material 7. INC MSE corresponds to the increase in the mean squared error of the predictions after permutation. INC Node Purity is the average decrease in node impurity measured as residual sum of squares. Both are used to assess the importance of predictors in an RF model. The higher the value of both measures, the more important the variable.

Response variable	Variance explained (%)	Variable	INC MSE (%)	INC Node Purity
Total terrestrial plant litter (TPL)	41.4	Aridity	31.9	34.9
		Rain	29.1	36.4
		Catchment area	25.3	34.2
		Duration of dry period	19.6	25.7
Leaf litter (LL) .	38.3	Aridity	47.4	23.8
		River channel width	40.8	26.7
		Riparian cover	37.2	23.8
		Time since senescence	30.6	19.1
		Duration of dry period	30.3	26.5
C:N	14.9	PET	63.5	2.9
		Duration of dry period	48.3	2.1
		Riparian cover	47.6	2.1
		Aridity	42.2	2.0
Respiration rate	36.8	Riparian forest	68.6	0.3
		Catchment area	60.5	0.2
		Time since senescence	51.7	0.2
		Duration of dry period	48.2	0.2
		Aridity	38.7	0.1
		C:N	35.2	0.1
CO_2 release	31.9	Time since senescence_	57.7	38.3
		Aridity	49.7	27.3
		Duration of dry period	44.1	36.7

Figure captions.

Figure 1. Conceptual model of the main variables predicted to control plant litter accumulation and decomposability in intermittent rivers and ephemeral streams. The accumulation of terrestrial plant material is a function of the input of litter from riparian vegetation mediated by its retention that depends on channel topography and the duration of dry events. Channel topography and composition of the riparian vegetation are driven by flow regimes and, ultimately, climate. Climate also influences the condition of the litter accumulated during dry phases and hence its preconditioning. Photo credits: D. von Schiller (left panel) and M. Moléon (right panel).

Figure 2. Partial dependence of the probability of the quantity of leaf litter (LL) accumulated on dry riverbeds for the main predictors of random forest models. Variables are shown from the top left to the bottom right in order of decreasing importance. The plots show the marginal contribution to probability of the quantity of LL accumulated in dry reaches (marginal response, y-axis) as a function of the predictors (i.e. when the other contributing predictors are held at their mean). The rug plots on the horizontal axes show deciles of the predictors.

Figure 3. a. Partial dependence of the probability of the CO_2 released by rewetted leaf litter (LL) over 24 h for the main predictors of random forest models. Variables are shown from left to right in order of decreasing importance. The plots show the marginal contribution to probability of the CO_2 released by rewetted LL over 24 h (marginal response, y-axis) as a function of the predictors (i.e. when the other contributing predictors are held at their mean). The rug plots on the horizontal axes show deciles of the predictors. **b. CO_2 released mapped onto the original sampling reaches.**

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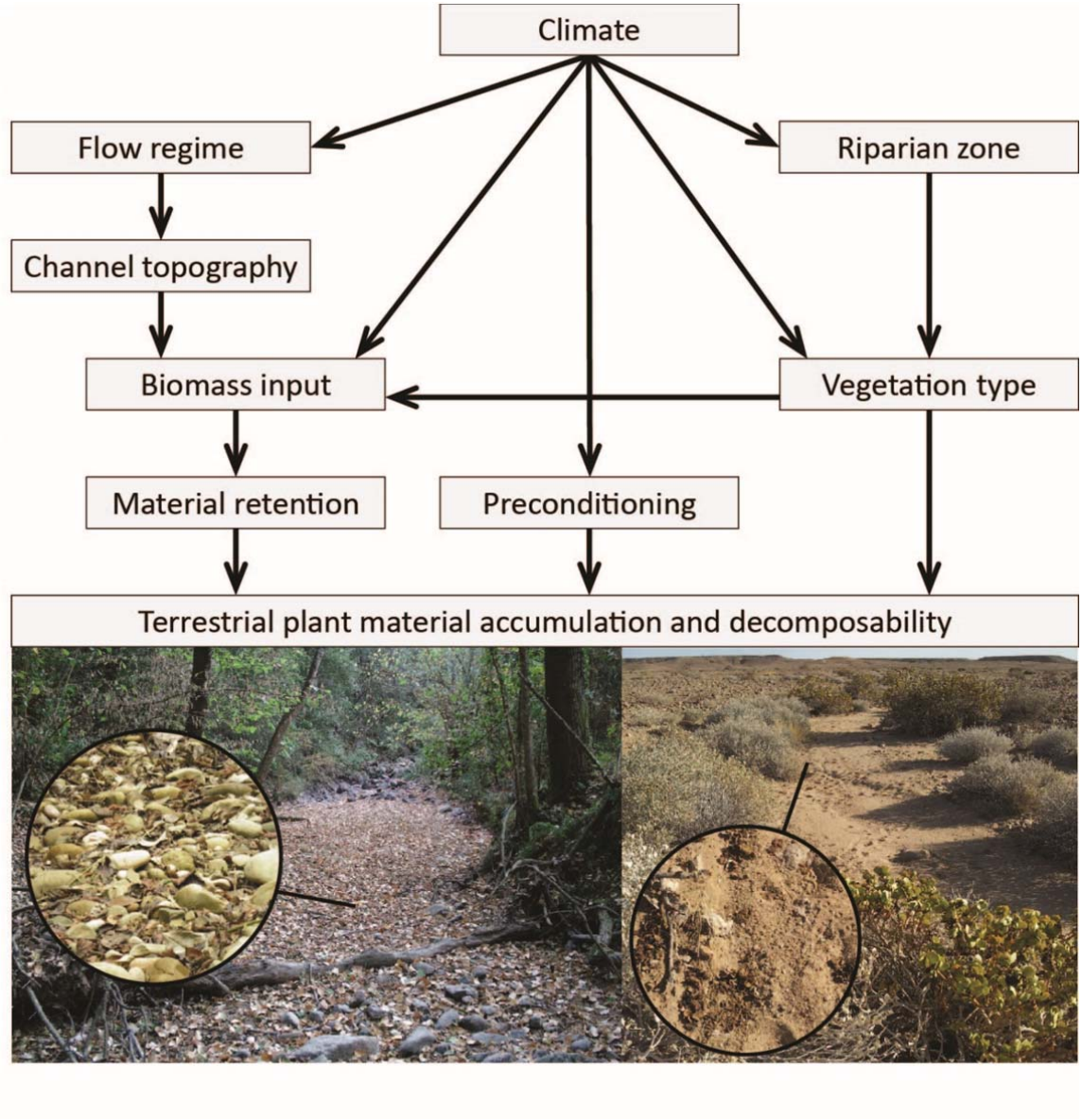

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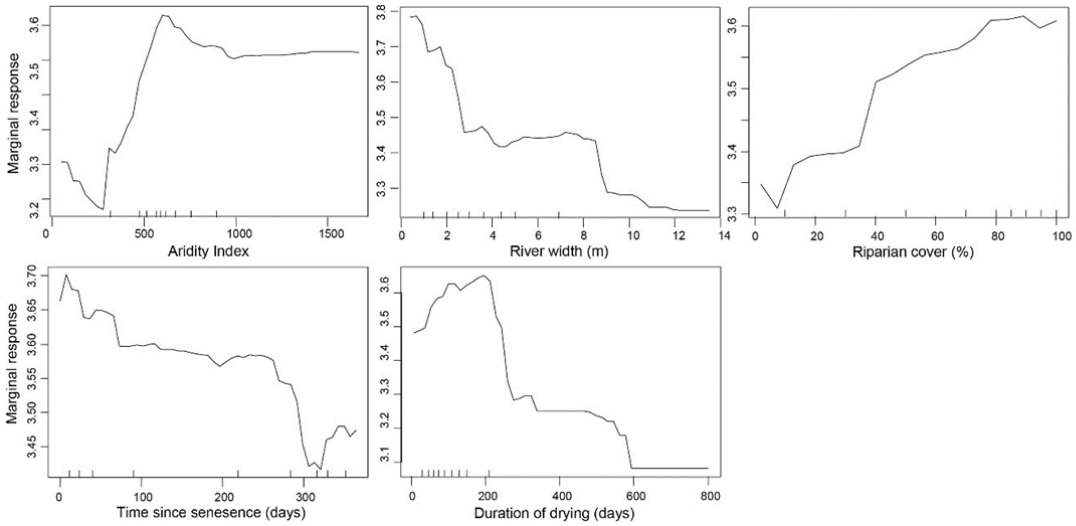
475 Figure 1



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478 Figure 2.

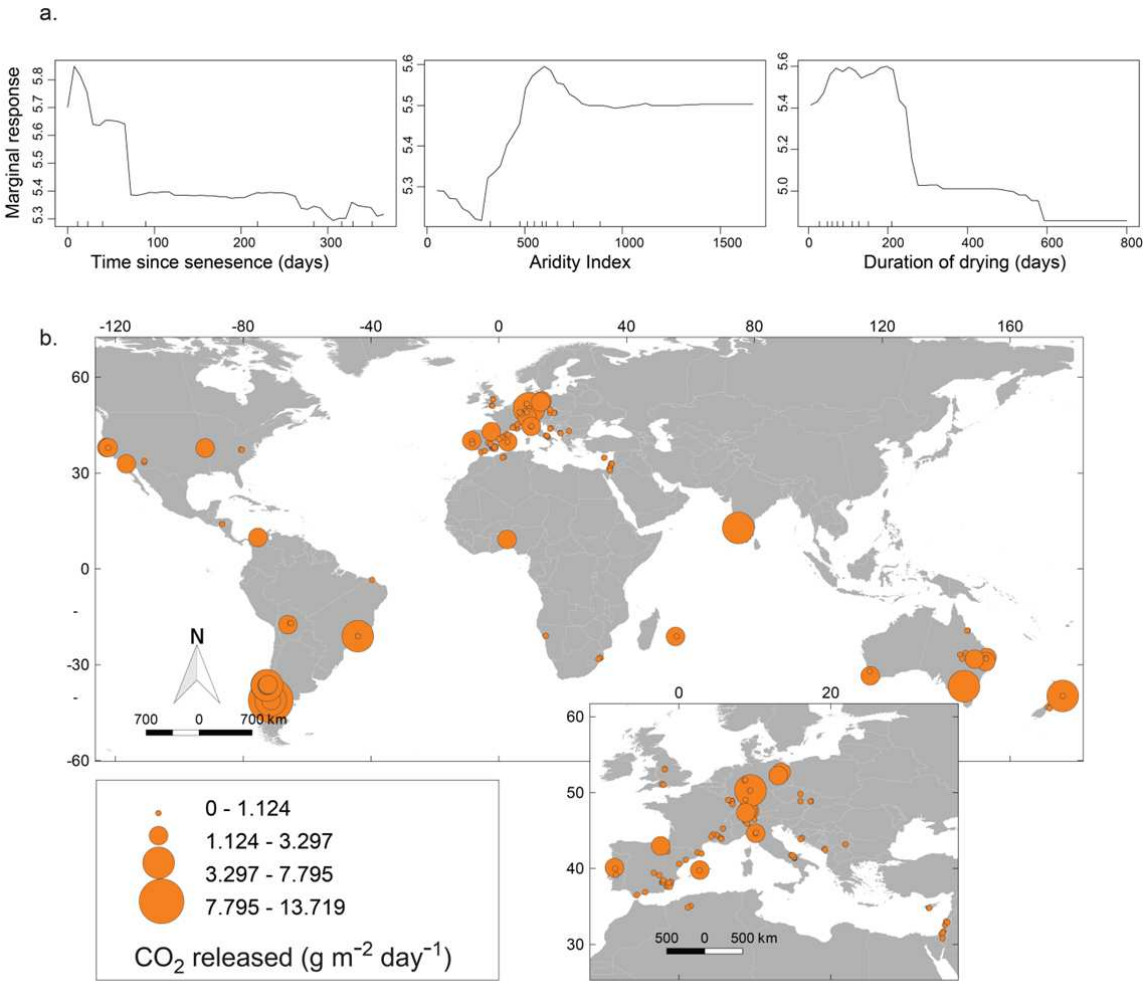
a.
Marginal response
Time since senesence (days)
Aridity Index
Duration of drying (days)
b.
N
700 0 700 km
0 - 1.124
1.124 - 3.297
3.297 - 7.795
7.795 - 13.719
CO2 released (g m-2 day-1)
500 0 500 km

Figure 3.